Predicting the spatial and temporal effects of climate change on the south american lizard genus *Teius* (Squamata: Teiidae)

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Background. The consequences of past or future climate change have been studied in many physical and biological systems, and their effects could change the ecology and spatial distribution of suitable areas for a wide variety of organisms.

Methods. We analyzed the environmental and geographic space of the current suitable area and we projected these conditions into Mid-Holocene and 2050 RCP8.5 scenarios. Through these projections, we assessed and quantified whether climate change would affect the distribution and size of environmental and geographic space for lizard species of the genus *Teius*.

Results. The potentially suitable geographic area for the Mid-Holocene decreased for *T. oculatus* (-29.55%) and for *T. teyou* (-6.82%), but for *T. suquiensis* it was inferred as a larger suitable area (+26%). For the future scenario all species showed a decrease in the potentially suitable area compared to the present (*T. oculatus* = -9.30%, *T. teyou* = -0.79%, *T. suquiensis* = -37.58%). The first 3 PCA axes in the environmental space explained more than 86% of the variation for each temporal scenario for all species. The higher contribution for PC1-2 in Mid-Holocene and Present were mostly related to temperature and for PC3 with altitude variables: and for the 2050 scenario were temperature for PC1, precipitation for PC2 and altitude-temperature for PC3. The hypervolumen distance for *T. oculatus* from the Present scenario to Mid-Holocene = 67.80 and for 2050 = 309.10; for *T. teyou* to Mid-Holocene = 95.67 and for 2050 = 442.67; for *T. suquiensis* to Mid-Holocene = 275.57 and for 2050 = 248.07.

Discussion. These results suggest that current geographic space versus the other temporal forecast of all *Teius* species, showed different specific magnitude changes in their potentially suitable areas. This work illustrates how ectothermic organisms might have to face major changes in their environmental and geographic space as a consequence of the effect of climate changes.

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ABSTRACT

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Keywords: niche modeling, climate change, Mid-Holocene, 2050 scenario, reptiles, *Teius*.

INTRODUCTION

The concept of ecological niche has long been considered to be an important factor in the species' distribution range and was defined as a set of environmental conditions that maintains each taxon within a certain geographic range, modulated by physiological restrictions under which they can prosper (Grinnell, 1917; James et al., 1984). Numerous works studied this concept in recent decades from the theoretical point of view (Soberón & Peterson, 2005; Peterson et al., 2011) and in general they agree that it includes certain components and they are commonly summarized in the BAM diagram. The BAM framework (Soberón & Peterson, 2005) for a species includes a region with a suitable set of abiotic factors (A) and this represents the geographic expression of the fundamental niche (FN), a region with appropriate biotic interactions (B), a region "accessible" to colonization (M) and a region equivalent to the distribution of the species (P) which is the intersection of the three identified regions ($P = A \cap B \cap M$). The niche concept is commonly separated into two major classes: Grinnellian and Eltonian niches. The Grinnellian niche (Grinnell, 1917; Austin, 2002; Soberón, 2007) is defined mainly by abiotic and non-interactive variables, while biotic interactions and resources define the Eltonian niche (Elton, 1927; Vandermeer, 1972; Leibold, 1995). Usually, these concepts and theoretical frameworks are not taken into account by researchers that model species' niches (Townsend Peterson & Soberón, 2012).

In the past decades, a large number of scientists estimated spatial distributions by calculating and quantifying "environmental" or "ecological" niches (Colwell & Rangel, 2009; Soberón & Nakamura, 2009), mostly through mechanistic and correlative models. The analysis of the niche through mechanistic models allows to evaluate a physiological limitation and to project it into the geographic space (Sinervo et al., 2010), while the correlative models perform correlations between several variables and the distribution of the studied organism (Owens et al., 2013). Both types of models have advantages and disadvantages, but correlative models can analyze habitat suitability considering several environmental variables together. Habitat suitability modeling can be subjected to spatial analysis such as area calculation (Di Marco et al., 2016), importance of variables in the geographic distribution (Marino et al., 2011) and interaction of the variables with each other (Hirzel & Le Lay, 2008).

The study of present habitat suitability is an effective method to infer the spatial interactions and shifts of organisms with past and future climate changes (Peterson et al., 2011). Niche modeling analysis is frequently used in research dealing with species distribution, and is applied to assess geographic ranges within different evolution scenarios (Wiens & Graham, 2005; Warren, Glor & Turelli, 2008); as a tool for biodiversity conservation (Hortal et al., 2015; Jones et al., 2016; Tulloch et al., 2016), or to predict distributions under diverse climate scenarios events (Barrows, 2011; Anderson, 2013). Given the evidence of impact of climate change on biodiversity and on the fate of species' survivorship, there was an eruption of papers focused on this topic, and many scientists made simulation models and predictions based on the climate shift scenarios (Cane, 2005; Parker, 2010). Several resources, software and algorithms were produced in the last two decades to perform modeling and simulations (Thuiller et al., 2009; Di Cola et al., 2017) using climatic layers (e.g., Lima-Ribeiro et al., 2015) to assess the effect of climate change on species' distribution.

The abiotic factors can determine regional and local patterns by which communities of organisms are assembled, and the resulting degree of similarity or difference between localities with similar environments (Chase, 2003). Studies on changes of the potential suitable abiotic area for a species, have been mostly focused on the geographic space and to a lesser extent in the environmental space (Soberón & Nakamura, 2009; Owens et al., 2013). Ectothermic organisms, and particularly reptiles are susceptible to climate changes (Sinervo et al., 2010; Böhm et al., 2016). Lizards are an optimal study object to test the climate changes effects, since this group of ectotherm organisms is highly susceptible to climate change (Kubisch et al., 2015) or habitat destruction, because of their reproductive strategies and low dispersal capacity (Zajitschek, Zajitschek & Clobert, 2012). Therefore, the analysis of displacement and contraction of the appropriate climatic-environmental areas for lizard species with little physiological adaptability is a major research goal (Huey et al., 2012; Ceia-Hasse et al., 2014).

In this study, we evaluated the potential effects of climate shifts projected for Mid-Holocene and 2050, in the lizard genus *Teius* using ecological niche modeling (ENM, sensu Townsend Peterson & Soberón, 2012), considering the two aspects of Hutchinson's duality: geographic and environmental spaces (sensu, Soberón & Nakamura, 2009). The geographic projection of present modeled distributions coupled with comparisons with ~6000 years ago conditions versus a future medium-term model of 35 years, could provide solid evidence of the niche's shift magnitude in asymmetric time ranges modulated by climate change. The objectives of this study for these taxa were i) to analyze and quantify the current available area with habitat suitability models, and assess potential spatial changes projecting these conditions onto two temporal scenarios: Mid-Holocene (~6000 years ago) and the 8.5 Representative Concentration Pathway greenhouse gas concentration (RCP8.5) for 2050; and ii) evaluate changes in the environmental space through n-dimensional hypervolume analysis for the three species, the overall genus, and the three scenarios.

MATERIALS AND METHODS

Studied species and localities data

The genus *Teius* include three species that geographically range from 40° S in Argentina to Uruguay, Paraguay, and the southeastern region of Brazil and Bolivia at 16°40’ S (Cacciali et al., 2016b,a). These species are relatively large and robust (~144 mm. snout-vent), diurnal, carnivorous and oviparous (Cei, 1993). Within this genus, *T. oculatus* and *T. teyou* present a wide distribution in different environments in Argentina, Uruguay, Paraguay and Brazil (Cacciali et al., 2016a). *Teius suquiensis* has a restricted distribution in central Argentina that partially overlaps with the other two taxa (Cabrera & Monguillot, 2007).

We used 1037 georeferenced presence records (*T. oculatus* = 581; *T. suquiensis* = 52; *T. teyou* = 404) from 675 localities. We obtained this information from the herpetological collection of reptiles (LJAMM-CNP) from Instituto Patagónico para el Estudio de los Ecosistemas Continentales - Centro Nacional Patagónico - CONICET (Puerto Madryn, Chubut, Argentina). Collections acronyms and voucher specimens are cited in Cacciali et al. (2016a). Species sampling, observations and collecting events tend to be clustered around accessible areas and roads. This may overestimate modeling results by including localities that are not spatially independent and do not present environmental variation between them (Dormann et al., 2012). For records with no exact or available geographic locations, we only incorporated them when it was possible to assign approximate coordinates according to the detailed descriptions of locations as they appear in the museums records and literature.

Climate and environmental data

We modeled habitat suitability for each species through a selection from the 19 bio-climatic variables for current conditions (~1950-2000) and included an altitude variable from the data base WorldClim 1.4 - Global Climate (http://www.worldclim.org). We projected current modeled conditions to BCC-CSM1-1 bioclimatic layers (PMIP2, 2009) for the Mid-Holocene scenario (~6000 years ago) and ACCESS1-0 CMIP5 (2015) layers for modeling 2050 scenarios with RCP8.5 concentrations. The layers for these temporal scenarios were downscaled and calibrated (bias corrected) by their authors through a database using WorldClim 1.4 as baseline 'current' climate (WorldClim - Global Climate Data, 2015). All used layers had a resolution of 30 arc-seconds (~1 km^2). The IPCC performs simulations of the climate system response to increasing levels of greenhouse gases based on different assumptions about the size of the projected population, technological developments and socio-economic trends. The RCP8.5 scenarios projected relatively large changes based on the most recent observations, which suggested that climate change would be more severe than expected (Meehl et al., 2007; Rahmstorf et al., 2007; Smith et al., 2009).

We estimated the accessible area (M; sensu Barve et al., 2011) considering ecological traits, environmental features and potential historical distribution to generate an extent for each taxon. We initially considered the ecoregions as M, but many presence records were located on the edge of these regions, hence we defined M as a minimum convex polygon with an additional spatial buffer of 200 km for each species. Then, we used these extent sizes to clip the environmental layers and generated 5000 random points for each species, and we extracted the pixel values for each bio-climatic variable for both species from these random points and we used them to create a subset of variables. In order to obtain a representation of both types of climatic variables (Barbet-Massin & Jetz, 2014), we divided them in two groups: 1- precipitation and 2- temperature. We evaluated the number of variables to use implementing an initial Jackknife test (Pearson et al., 2006). Then, for each variable group we performed a Spearman correlation test (threshold selected > 0.75) to avoid collinearity (Debandi et al., 2012; Dormann et al., 2013; Kershaw et al., 2013) and additionally a selection criterion with biological significance for the studied species (Rissler & Apodaca, 2007; Debandi et al., 2012; Cacciali et al., 2016a) related to the active months period. We performed all correlation analysis with Ggally 1.0.1 R package (Schloerke et al., 2016).

Ecological niche models (ENM)

We generated correlative models of ENM using MaxEnt (3.3.3k version; 2016) algorithm, which seeks maximum entropy density (Merow, Smith & Silander, 2013) through a robust estimation requiring only presence records (Phillips, Anderson & Schapire, 2006; Phillips & Dudík, 2008; Elith et al., 2011) and supports a low number of localities (Pearson et al., 2007; van Proosdij et al., 2016). With this software, we calculated the relationship between the current presence of each species and environmental variables, and projected them into the a past and future scenarios. We ran MaxEnt using the selected subset for each species of bio-climatic and altitude variables with the default configurations, except for: 10 replicates, 1000 Maximum iterations, "10 percentile training presence logistic threshold" as selected threshold for each average model.

We evaluated the ENMs performance with true skill statistic (TSS) for model's replicates (Allouche, Tsoar & Kadmon, 2006; Lobo, Jiménez-Valverde & Real, 2008) and Area Under the Receiver Operator Curve (further abbreviated to AUC; Phillips, Anderson & Schapire, 2006; Elith et al., 2011) for the averaged models. TSS takes into account both omission and commission errors and success as a result of random guessing, hence this evaluation model is not affected by prevalence and also is not affected by the size of the validation set (Allouche, Tsoar & Kadmon, 2006). The TSS values ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche, Tsoar & Kadmon, 2006). We considered these values as TSS model performance indicators: < 0.05 – 0.05 no agreement, 0.06 - 0.39 = poor, 0.40 - 0.55 = fair, 0.56 - 0.70 = good, 0.71 - 0.85 = very good, 0.86 - 0.99 = excellent, 0.99 - 1 = perfect (following Monserud & Leemans, 1992). The AUC is a measure of rank-correlation and high AUC values indicates that sites with high predicted suitability values tend to be areas of known presence and locations, whereas a model with lower prediction values tend to be areas where the species is not known to be present (absent or a random point). An AUC score of 0.5 means that the model is as good as a random guess. We considered AUC range values to interpret model performance sensu Araújo et al. (2005): excellent ≥ 0.90; good ≥ 0.80; fair ≥ 0.70; poor ≥ 0.60; fail ≤ 0.50. Finally, we created binary maps based on the selected threshold on the current average models and projected them to onto the Mid-Holocene and 2050 RCP8.5 scenarios.

Geographic space, spatial analyses and potential effects on adequate areas

We used the suitable habitat from the final output models to quantified the area for each species and scenario. From these surfaces, we calculated impact metric to estimate specific distribution changes of predicted suitable areas and the exposure to climate change per species and the overall genus. We analyzed the relative exposure to climate change (Recc) between the current surface models (Cm) versus past (Pm) and future models (Fm) as: Recc = (Pm * 100 / Cm) – 100 and Recc = (Fm * 100 / Cm) – 100 respectively. Thus, high negative relative exposure values indicate that a species decreases the suitable area in that scenario, whereas higher positive values indicate an increase of the suitable area. The estimation and comparison of areas to estimate changes in the different modeling scenarios is a widely implemented method in ENM (e.g., Nori et al., 2013; Nori, Carrasco & Leynaud, 2014; Bonino et al., 2015; Rubio-Salcedo et al., 2016). This might be interpreted as a rigid and conservative estimate of changes from the predicted suitable areas, since we did not considered areas of recolonization after a potential disappearance of suitable environment. Given that there is almost no published literature on the spatial ecology of these species, our analyzes were based on the assumption that none of these lizards would be able to disperse to new potentially suitable areas within the time period of the model. These assumptions were considered due to lack of ecological information on its dispersal ability and adaptability to all the bio-climatic variables considered in the models. These kind of assumptions are commonly associated with forecasting modeling niche techniques (Araújo & Pearson, 2005; Elith & Leathwick, 2009).

We performed all spatial analyses and maps with “raster 2.5-2” (Hijmans, 2015b), “maptools 0.8-39” (Bivand & Lewin-Koh, 2016), “sp 1.2-2” (Pebesma & Bivand, 2016), “rgdal 1.1-7” (Bivand, Keitt & Rowlingson, 2016), “geosphere 1.5-1” (Hijmans, 2015a), “rgeos 0.3-17” (Bivand & Rundel, 2016) R packages.

Environmental space and n - dimensional hypervolumes

We evaluated changes in the environmental space for each of the species considering visualization results and metrics between the n - dimensional hypervolumes obtained from the geographic suitable outcome area for each of the model's scenarios. The environmental space state is a complex system that involves interactions for more than two variables and can be described as an n - dimensional cloud of points or an n - dimensional hypervolume (Soberón, Osorio-Olvera & Peterson, 2017). If these environmental space conditions are disturbed, it might lead these variables to take other values and to produce a different n - dimensional hypervolume; hence the comparison of two or more hypervolumes could provide an assessment of the magnitude of changes that the ecosystem suffered, such as shifts from the initial state (Blonder et al., 2014). In order to do this, we followed the "framework to study ecosystem stability in face of environmental changes using n - dimensional hypervolumes" (*sensu*, Barros et al., 2016). Within this framework, we calculated two metrics to made hypervolumes comparisons: 1- the proportion of overlap between pre and post perturbation hypervolumes will reflect overall differences between the two corresponding states, 2- the distance between the centroids of the pre and post perturbation hypervolumes will reflect how much mean values of the ecosystem components have departed from their pre perturbation levels (changes in mean values) and 3- the contribution of the variables to each retained component.

To accomplish these analyses, we randomly sampled points (= number of localities * 10) from each of the species' suitable area, and we used these random points to extract the information from the sum of the individual layers employed in MaxEnt for each taxon. Then, all this environmental information for each species was compiled and we performed a Principal Component Analysis (PCA) per scenario, to quantify the ecological multivariate space from the variables that determine the geographic models, and explore how these spaces interacted among the three taxa through time. To improve the visualization of the points, we incorporated gridded ellipses including 95% of the observations for each factor level. We used "The Scree Test" and "Proportion of Variance Accounted For" criteria and components that explain a minimum of

~10% of the variation (O'Rourke & Hatcher, 2013), to decide how many PCA axes we had to consider for this analysis. For these given dimensions, we evaluated the variables' contributions with the function "fviz_contrib". This function calculates any row/column with a contribution above the reference threshold, under which it could be considered as an important variable in contributing to the n - dimensions taken into account (see, Kassambara & Mundt, 2017). We compared the hypervolumes implementing the algorithm "hypervolume_distance" which calculates the Euclidean distance between two hypervolumes centroids (see, Blonder, 2015). We performed all environmental space analyses with "FactoMineR 1.34" (Lê, Josse & Husson, 2008), "factoextra 1.0.4.999" (Kassambara & Mundt, 2017), "hypervolume 1.4.1" (Blonder, 2015), "car 2.1-4" (Fox & Weisberg, 2011), "ade4 1.7-5" (Dray & Dufour, 2007), "rgl 0.96.0" (Adler & Murdoch, 2017) R packages.

RESULTS

ENM, spatial analyses and potential temporal shifts in suitable areas

Considering the bio-climatic correlation analysis outcome, we selected altitude and these environmental variables for each species: *Teius oculatus*: bio1 (annual mean temperature), bio3 (Isothermality = (bio2 / bio7 * 100), bio5 (maximum temperature of warmest month), bio7 (temperature annual range = bio5–bio6), bio9 (mean temperature of driest quarter), bio17 (precipitation of driest quarter), bio18 (precipitation of warmest quarter); *T. suquiensis*: bio2 (mean diurnal range = (mean of monthly (maximum temp – minimum temp)), bio3, bio4 (temperature seasonality = (standard deviation*100)), bio5, bio6 (minimum temperature of coldest month), bio15 (precipitation of seasonality = (coefficient of variation)), bio18; *T. teyou*: bio2, bio3, bio4, bio5, bio15, bio17, bio18. The replicates performance through TSS indicated models fitted above "fair" or "good", with relatively high values for most of the replicates in the three species (Fig. S.1, supporting information). The average test AUC for replicate runs for

Teius oculatus was 0.763 (± 0.028 SD), 0.922 (± 0.043 SD) for *T. suquiensis*, and 0.797 (± 0.028 SD) for *T. teyou*.

The suitable climate area in Present scenario was 748,911.98 km^2 for *Teius oculatus*, 104,209.16 km^2 for *T. suquiensis* and 926,690.31 km^2 for *T. teyou* (Fig. 1). The Recc for *T. oculatus* Mid-Holocene scenario suitable area showed a reduction of 29.5 % and 9.30 % for 2050 RCP8.5 (Fig. 1); but *T. teyou* Recc presented a moderate decrease in both past and future scenarios with a reduction of 6.82 % and 0.79 % respectively (Table 1, Fig. 1). The Mid-Holocene models Recc for *T. suquiensis* indicated a 26 % higher suitable area than the Present scenario and a reduction of 37.58 % for 2050 RCP8.5 (Table 1, Fig. 1). All species did not show future considerable differences in changes of latitude or longitude (Fig. 1). The relative exposure to climate change (Recc) for different scenarios and suitable area shifts for *Teius* are detailed in Table 1.

Environmental space

We observed changes in the environmental space for all the studied species. Principal component analysis indicated that most of the hypervolumes variation could be explained by the first three components for the 3 studied scenarios. The first three axes accounted for all scenarios a variance over 86% of the variation for each temporal scenario (Table 2). The variables that most contributed in Mid-Holocene and Present were BIO6, BIO7 and BIO 4 for PC1; BIO17, BIO1, BIO15 and BIO5 for PC2; and BIO3, BIO5, and altitude for PC3. For the 2050 scenario the variables with higher contribution for PC1 were BIO7, BIO9, BIO4, BIO6; for PC2 BIO, BIO17, BIO15; and altitude, BIO5 for PC3 (Fig. 2). The hypervolumen distance for *T. oculatus* from the Present scenario to the Mid-Holocene = 67.80 and to the 2050 = 309.10; for *T. teyou* to the Mid-Holocene = 95.67 and for the 2050 = 442.67; and for *T. suquiensis* to the Mid-Holocene = 275.57 and to the 2050 = 248.07. These changes in the ellipses for each of the analyzed angles (Fig. 3), were moderate between the Mid-Holocene and the Present scenario. On the other hand, the

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ellipses of the Present and 2050 scenarios showed considerable changes between them, especially for *T. teyou* and *T. suquiensis* (Fig. 3).

DISCUSSION

We found strong support for Grinnellian niche shifts in the past and future scenarios for *Teius* species. The geographic space from an ENM does not exclusively underlie on abiotic variables and, on the contrary there are several factors that determine it (Peterson et al., 2005; Soberón & Peterson, 2005). Despite this, the Grinnellian niche is a good approach to study the relationship between climatic changes and areas suitable for the species' presence without introducing biases of non-climatic aspects (Larson, Olden & Usio, 2010; Chalghaf et al., 2016). Our results, in congruence with other published works related to climate change in lizards (Ballesteros-Barrera, MartÍnez-Meyer & Gadsden, 2007; Kaliontzopoulou et al., 2008; Winck, Almeida-Santos & Rocha, 2014) and amphibians (Lemes, Melo & Loyola, 2014; Zank et al., 2014; Vasconcelos & Do Nascimento, 2016), showed a general tendency toward a higher potentially adequate habitat in the past scenario (Fontanella et al., 2012; Sillero & Carretero, 2013; Breitman et al., 2015) and a reduction for the future (Araújo, Thuiller & Pearson, 2006; Bonino et al., 2015; Minoli & Avila, 2017).

Although the studied genus inhabits environments from a wide geographic space, our findings supported the hypothesis that the suitable area changes as the result of exposure to climate change (Vera-Escalona et al., 2012; Minoli & Avila, 2017). Comparing the spatial forecasts among the studied species, *T. teyou* and *T. oculatus* showed less reduction of their potential future area than *T. suquiensis*, which presented high Recc values resulting in a major reduction of the potential future area. In addition, these findings support the theoretical framework which states that each species has its own niche area (Medina, Ponssa & Aráoz, 2016) and magnitude of response to potential changes in their Grinnellian niche (Colwell & Rangel,

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2009; Soberón & Nakamura, 2009). Although the differences between the results may be due to possible sampling bias (Syfert, Smith & Coomes, 2013), the distribution employed here is the complete currently known for the genus.

Spatial barriers in reptiles (Sahlean et al., 2014) and potential changes in the distribution of suitable areas and their inter-species overlaps (Barbosa et al., 2012), have been extensively documented and related to hypotheses about hybridization events as a consequence of this phenomenon (Engler et al., 2013; Ahmadzadeh et al., 2013). The most important finding in the geographic context, were the changes in the potential suitable habitat of the *T. suquiensis*, which currently has a broader distribution range. This parthenogenetic species showed significantely changes in both geographically and ecological space with a noticeable tendency towards the reduction of adequate area through temporal scenarios (Fig. 1, Fig. 3, see supplementary files). Our results support that this species showed the greatest decrease of potentially suitable areas for the future, and even the suitable northern sector for the present model would disappear in the future scenario. The unisexual species could arise from hybrid individuals and they are from a recent origen, perhaps within ten thousands of years (Moritz et al., 1992). The unisexual species would be expected to have a shorter persistence than sexual species, and to colonize and occupy ecotone habitats more quickly compared with their sexual relatives (Pough et al., 2015). Moreover, potential contractions for the species's suitable areas should be taken with great attention as there are multiple factors (e.g., anthropic changes, such as oil extraction, cultivated soils, dams, desertification) that could play a decisive role increase the effects to materialize these shifts (Bastos, Araújo & Silva, 2005; Nori et al., 2013). We consider that new field surveys are needed because this is one of the sectors that would be lost in the 2050 scenarios.

The limited knowledge of these species' dispersion or fossil records combined with the great fragmentation and degradation of the environments they inhabit (Pelegrin et al., 2009, 2013; Pelegrin & Bucher, 2012), leads us to think that some of the suitable climate spaces predicted in our results for temporal scenarios remains uncertain whether they can be occupied or not (Araújo & New, 2007; Colwell & Rangel, 2009). Despite this, past or future impacts of climate change keep a moderate uncertainty level being influenced by interactions and effects of biotic, abiotic, and dispersal considerations (Townsend Peterson, Papeş & Soberón, 2016), the robustness of the models presented here were supported by the definition of the segment (i.e., Grinnelian) of the niche studied (Soberón, Osorio-Olvera & Peterson, 2017) and by the use of open algorithms which explains in detail their calculations (Phillips et al., 2017). These constraints of employed models could be mitigated and provide accurate forecasts of the lost-gain of the suitable geographic and climate spaces with a good sample of species presences and correct methodological choices, which increase the certainty of the predictions (Radosavljevic & Anderson, 2014).

CONCLUSIONS

In the last two decades several authors have done review works of ENM concepts (Soberón & Nakamura, 2009; Rangel & Loyola, 2012; Townsend Peterson & Soberón, 2012; McInerny & Etienne, 2012a,b,c), advantages and disadvantages of correlative, mechanistic and process-oriented models (Rangel & Loyola, 2012). Moreover, some authors propose blurry boundaries among these approaches (Dormann et al., 2012), and consider that these three approaches do overlap and interconnect (e.g., correlational niche estimates being used in process-oriented approaches). The additional advantages of using correlative models that we have implemented is to analyze a wider range of dimensions that define the niche the study object, but the biggest disadvantage is not being able to evaluate physiological thresholds as mechanistic models (Townsend Peterson, Papeş & Soberón, 2016). Until present, there have been numerous publications that used ENM as a tool to predict temporal changes in the distribution of suitable environments in the geographic space and projected them onto another scenarios (Schwartz, 2012; Lemes, Melo & Loyola, 2014; Ruete & Leynaud, 2015; Jones et al., 2016; Allen &

Lendemer, 2016). However, the future challenge in these studies should be to perform methods or analyses with very detailed explanations in order to be repeatable in both geographical and ecological space to also obtain quantified results on how and how much the climate change affects species' distribution.

The information provided in this work highlights the importance of potential distribution in the geographic and ecological spaces as tools to better understand the processes linked to recent species contractions and expansions at the regional and local context. The information provided here also allows adding testable data for the use of some species as proxies for climatic changes in the past and in the future. Moreover, understanding the processes that are behind this kind of phenomenon in such a wide area of South America, is essential to understand biota changes through time in this subcontinent.

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Figure 1

Area models for suitability habitat from the averaged replications output.

Teius oculatus in blue, *T. suquiensis* in red, *T. teyou* in green and all the genus. Projection: WGS84, coordinate system: EPSG 4326. Crosses represent localities from each species.

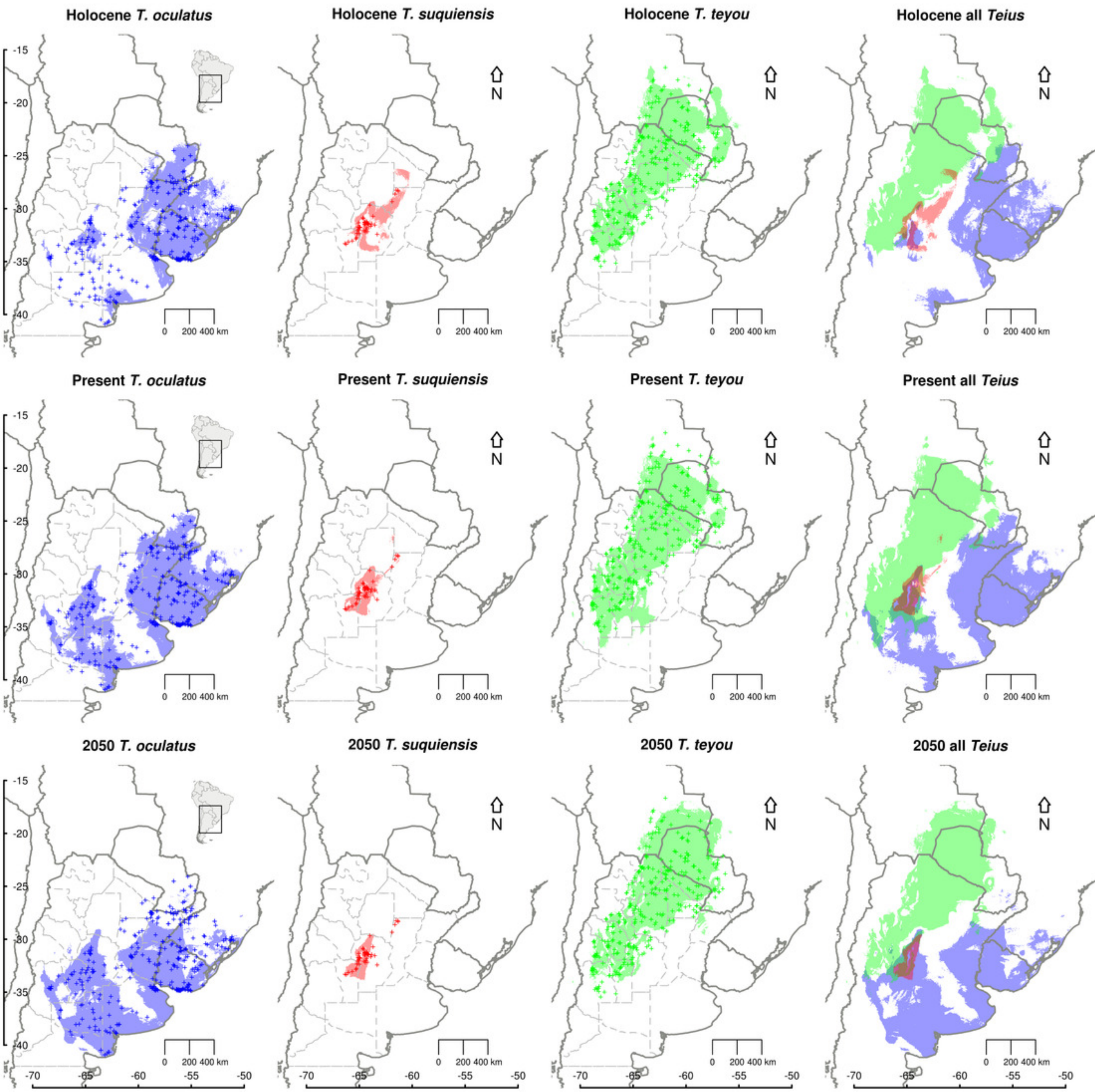

Figure 2

Barplot of variables contribution for the multivariate environmental space

Reference: dashed line corresponds to the expected value if the contribution where uniform between the considered dimensions.

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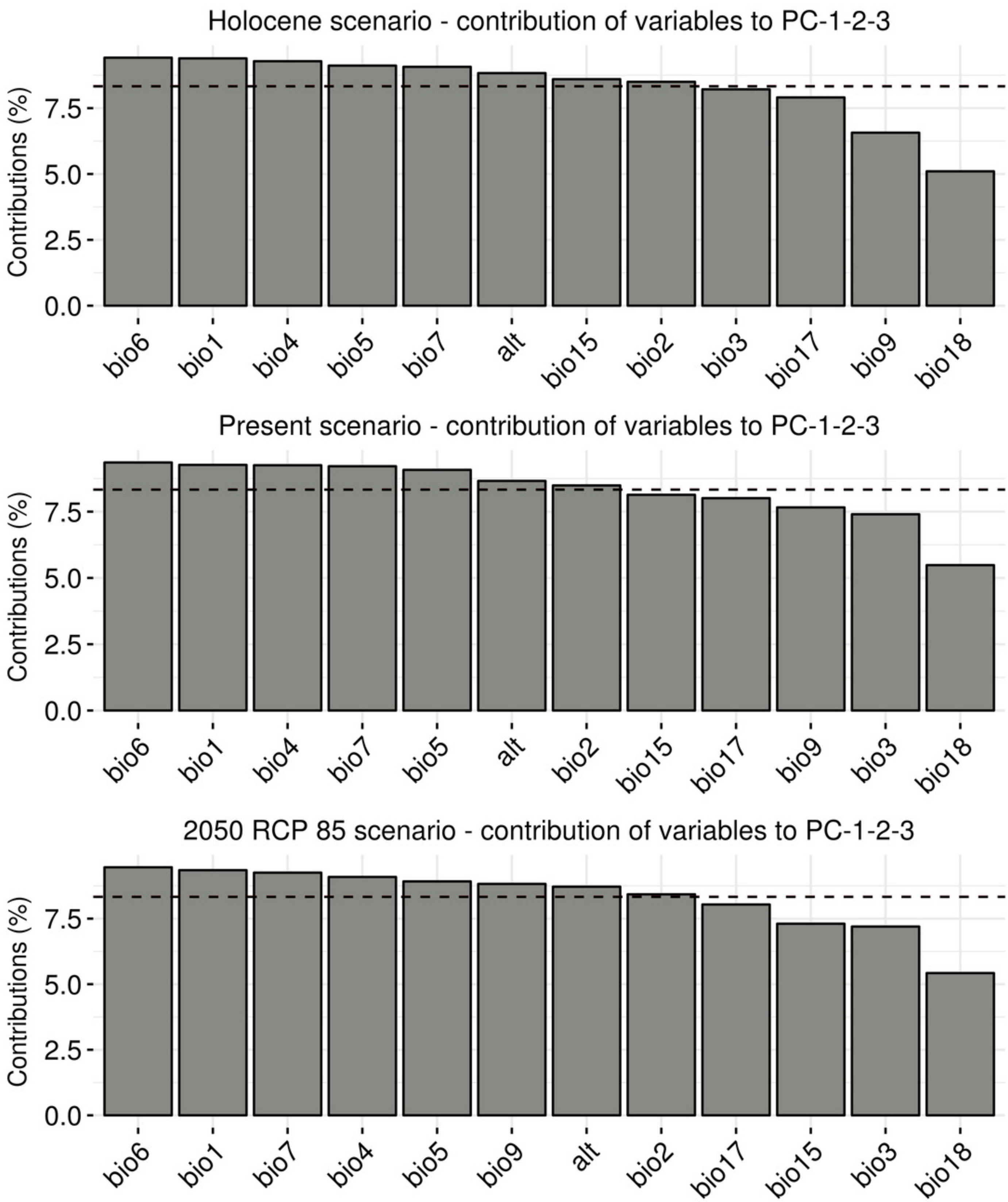
Holocene scenario - contribution of variables to PC-1-2-3
Contributions (%)
0.0
2.5
5.0
7.5
bio6
bio1
bio4
bio5
bio7
alt
bio15
bio2
bio3
bio17
bio9
bio18
Present scenario - contribution of variables to PC-1-2-3
Contributions (%)
0.0
2.5
5.0
7.5
bio6
bio1
bio4
bio7
bio5
alt
bio2
bio15
bio17
bio9
bio3
bio18
2050 RCP 85 scenario - contribution of variables to PC-1-2-3
Contributions (%)
0.0
2.5
5.0
7.5
bio6
bio1
bio7
bio4
bio5
bio9
alt
bio2
bio17
bio15
bio3
bio18

Figure 3

Changes of the environmental space in a multivariate context from the *Teius* studied scenarios

References: A) environmental space in a 0° degree view; B) environmental space in a 37° degree view; C) environmental space in a 74° degree view; D) environmental space in a 111° degree view. Colors: blue: *T. oculatus*; green: *T. teyou* and red: *T. suquiensis.*

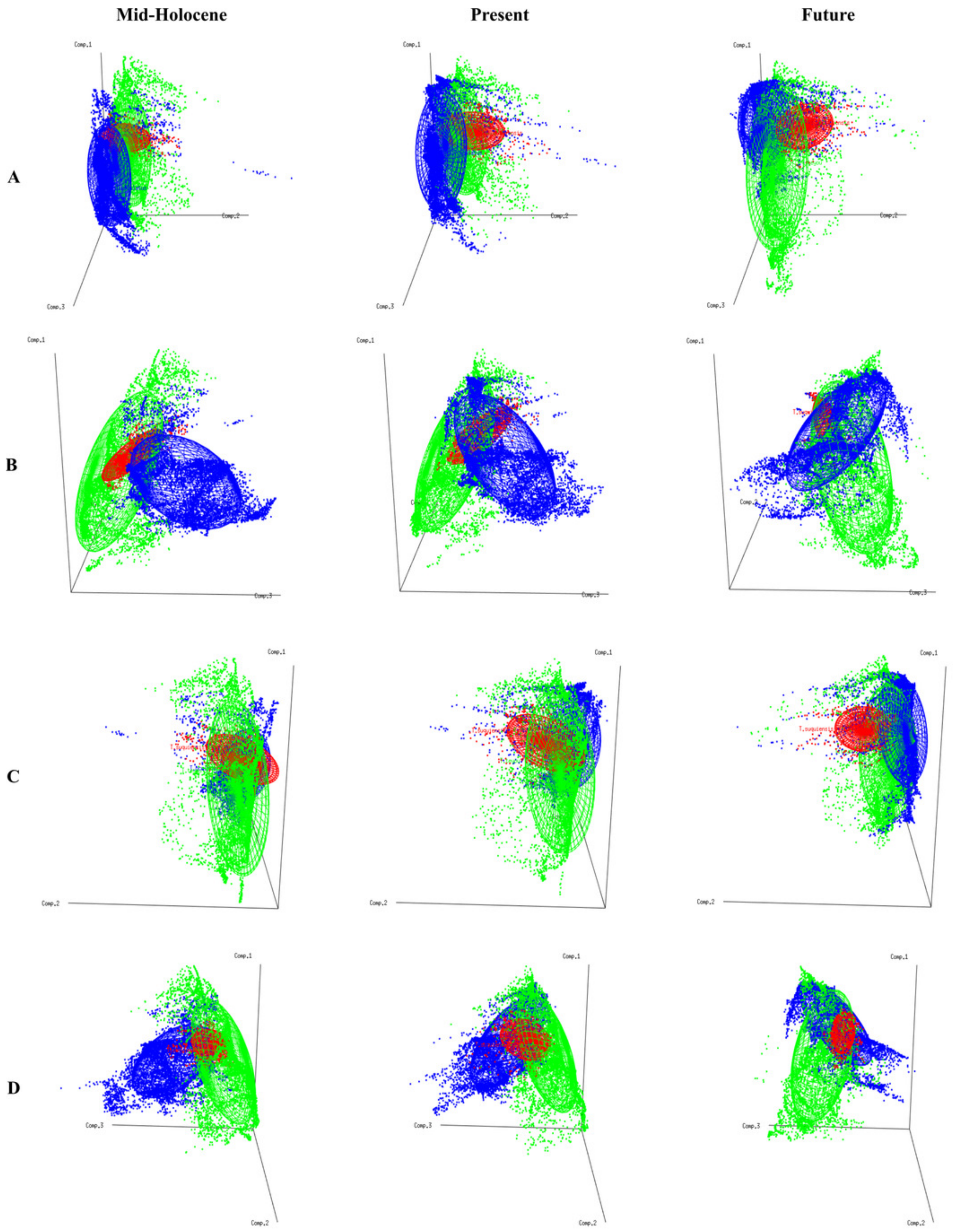
Mid-Holocene
Present
Future
A
B
C
D

Table 1(on next page)

Spatial analysis performed on output models for each time scenario.

References: % relative exposure to climate change (Recc) from present area.

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	Area (km^2)							
Scenarios	*Teius*	%	*T. oculatus*	%	*T. suquiensis*	%	*T. teyou*	%
Mid-Holocene	1,7174,23.23	-12.48	748,911.98	-29.55	104,209.16	26.00	926,690.31	-6.82
Present	1,962,427.11	-	1,063,106.79	-	82,708.09	-	994,568.05	-
2050	1,892,090.42	-3.58	964,195.47	-9.30	51,624.04	-37.58	986,697.77	-0.79

Table 2 (on next page)

Analysis of the environmental space.

Principal Component Analysis of the environmental space for each temporal scenario.

Holocene			
Axis	Eigenvalue	Variance %	Cumulative Variance %
PC 1	5.62	46.80	46.80
PC 2	3.62	30.20	77.00
PC 3	1.11	9.21	86.21
Present			
Axis	Eigenvalue	Variance %	Cumulative Variance %
PC 1	6.10	50.84	50.84
PC 2	3.16	26.34	77.18
PC 3	1.24	10.36	87.55
Future			
Axis	Eigenvalue	Variance %	Cumulative Variance %
PC 1	6.13	51.07	51.07
PC 2	3.19	26.59	77.66
PC 3	1.15	9.56	87.23

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